Cattle and Elk Responses to Intensive Timber Harvest

Michael J. Wisdom[1], Bruce K. Johnson, Martin Vavra, Jennifer M. Boyd, Priscilla K. Coe, John G. Kie, Alan A. Ager, and Norman J. Cimon

Introduction

Forested habitats for cattle and elk (Cervus elaphus) in the western United States have changed substantially in response to intensive timber management during the latter half of the 20th century. Consequently, the subject of how elk and other ungulates respond to timber management is a high-profile, long-standing issue that continues to be studied and debated (Lyon and Christensen 2002). The need for additional knowledge about effects of timber management on cattle and elk remains high, given the fact that timber management continues to affect nearly all cattle and elk ranges on National Forests in the western United States (Wisdom and Thomas 1996, Lyon and Christensen 2002).

Accordingly, we conducted a landscape experiment regarding cattle and elk responses to timber harvest and associated human activities at the Starkey Experimental Forest and Range (Starkey) (Figure 1) in northeast Oregon. Our specific objectives were to (1) summarize knowledge regarding cattle and elk responses to timber harvest; (2) document changes in spatial distributions and weight gains by these ungulates, and changes in elk vulnerability to hunting, as measured before, during, and after timber harvest at Starkey; and (3) describe management implications of our findings related to timber harvest planning.

Measuring Effects of Timber Management on Ungulates

We define timber harvest as "logging" activities that extract merchantable wood from forest stands; that is, tree felling and bucking and the subsequent yarding, decking, and hauling of logs for subsequent manufacture of wood products. By contrast, we define timber management as timber harvest and all other activities implemented in direct support of sustainable production of merchantable wood. Timber management therefore includes field layout of harvest units (cut units), such as marking trees and harvest boundaries; site preparation after timber harvest, such as prescribed burning, windrowing, and mechanical removal of fine fuels; seeding or planting of commercially-desirable tree seedlings after site preparation; and subsequent mechanical thinning of trees and other silvicultural treatments designed to enhance wood production.

Past research indicates that cattle and elk responses to timber harvest can change substantially in relation to four factors: (1) the types of response variables measured; (2) the spatial scales of measurement; (3) the time period following timber harvest, over which the response variables are measured (temporal scale); and (4) the confounding effects of other human activities associated with timber harvest, such as increased human activities from increased road access. Types of response variables can include estimates of change in ungulate behavior (Ward 1976), resource selection (Lyon 1976), or population performance (Leege 1976). Changes in habitat condition brought about by timber harvest, such as modification of biomass and quality of forage in relation to each ungulate's requirements, also have been studied extensively (e.g., Hershey and Leege 1976, Lyon 1976, Miller and Krueger 1976, Svejcar and Vavra 1985). Such differences in response variables in relation to timber harvest have contributed to differences in results and conclusions among various studies, leading to confusion about

[1] Suggested citation: Wisdom, M. J., B. K. Johnson, M. Vavra, J. M. Boyd, P. K. Coe, J. G. Kie, A. A. Ager, and N. J. Cimon. 2005. Cattle and Elk Responses to Intensive Timber Harvest. Pages 197-216 *in* Wisdom, M. J., technical editor, The Starkey Project: a synthesis of long-term studies of elk and mule deer. Reprinted from the 2004 Transactions of the North American Wildlife and Natural Resources Conference, Alliance Communications Group, Lawrence, Kansas, USA.

potential effects on ungulates. For example, documenting a change in ungulate habitat condition or habitat use in response to timber harvest says nothing about the effect on ungulate populations or their nutritional status (see discussion by Garton et al. 2001).

Similarly, the spatial scales at which ungulate responses are measured directly affect the interpretation of results (Boyce et al. 2002, Parker 2002). Spatial scale refers to the extent (boundaries and size of an area evaluated) over which an evaluation is conducted, and the mapping resolution (accuracy of each mapping unit, such as a pixel or polygon) at which a response is measured at a given extent (Turner et al. 2001, Gutzwiller 2002). For example, ungulate responses can be measured within a given stand that is subjected to timber harvest, or measured among a mosaic of stands that surround the area of harvest. Measurements of ungulate responses at the stand-level, versus a mosaic of stands encompassing the area of timber harvest, yield different but complementary insights (Boyce et al. 2002, Parker 2002).

One of the most important factors affecting ungulate responses to timber harvest is the temporal scale at which effects are measured. We define near-term effects as ungulate responses measured 1-10 years after timber harvest. We consider long-term effects as ungulate responses measured >10 years after harvest. Confounding the long-term responses of ungulates to timber harvest is the frequency of subsequent harvest activities. For example, if timber harvest occurs every 10 years in a given watershed, it may not be possible to measure a long-term response to any one set of harvest units beyond that of individual stands.

Perhaps the most challenging aspect to studies of timber harvest is the confounding effect of other human activities associated with harvest, such as road construction and the subsequent changes in human access. Increased human access can lead to increased hunting pressure on elk, owing to the larger network of roads established as part of timber management (Christensen et al. 1991, Unsworth et al 1993). Although these factors can be mitigated, such as with road obliterations or closures, the effects of such management activities are difficult to evaluate separately from the effects of other harvest activities, such as tree felling and bucking, during the time of harvest. By contrast, changes in human access resulting from timber harvest can be studied as a separate effect after harvest is completed.

Overview of Current Knowledge

Elk and other ungulates typically thrive in early-seral forests, owing to the high biomass of palatable forage produced under these open-canopy sites (see review by Wisdom and Cook 2000). Consequently, the increased forage produced by timber harvest could be perceived as a positive event to ungulates. Several factors however, provide confounding influences, both short- and long-term, complicating this perception.

Short-term disturbances by the act of timber harvest (Ward 1976, Edge and Marcum 1985), concomitant road building, and resultant traffic (Hershey and Leege 1976, Leege 1976, Perry and Overly 1976, Ward 1976) affect elk behavior. From a review of several studies, Lyon and Christensen (2002) found that elk are sometimes displaced from harvest areas by as much as 5 miles (8 km). Most often, however, the distance elk moved appeared to be the minimum required to avoid contact with people and equipment. Continual logging within an individual watershed (5 consecutive years) may impose learned behavior that delays return to previously used habitats (Lyon 1979). Edge et al. (1985) reported that home ranges of individual animals were not altered when areas of extensive cover remained available within their home range. The authors speculated that where cover is limited, harvest activities increase home-range size and reduce home-range fidelity.

Many studies support the concept that timber harvest is beneficial to forage production for elk and other wild ungulates (Hershey and Leege 1976, Leege 1976, Lyon 1976, Schroer et al. 1993, Unsworth et al. 1998). In the Coast Range of western Oregon, Crouch (1974) found that clearcutting and slash burning were the most practical means of maintaining black-tailed deer (Odocoileus hemionus columbianus) habitat, at no cost to wildlife managers. Continued harvest was required as forage production declined rapidly post-harvest because of the rapid regeneration rate of coniferous trees in the Coast Range.

Size of harvest units, however, has a substantial influence on subsequent forage use by ungulates. Scott et al. (1982) reported that small areas of disturbance are used more heavily than large ones. In that light, optimum size and arrangement of timber harvest units have been identified to maximize ungulate use of resulting forage areas. Lyon (1976) reported that harvest units of 10 to 40 acres (4 to 16 ha) were optimum. Reynolds (1966) found elk use was heavy on clearcuts <20 acres (<8 ha) in size, but use declined as opening size increased. Lyon and Jensen (1980) suggested that elk are more prone to use large harvest units in regions where large natural openings occur. Edge and Marcum (1991) suggested that both topography and forest cover should be considered in the development of logging operations and road placement. Wisdom et al. (1986) and Thomas et al. (1988) summarized knowledge of elk use in relation to edges between forage and cover areas, showing that highest use occurs within 100 yards (91 m) of such edges, decreasing with distance from the edges. These summaries supported the earlier guidelines established by Black et al. (1976) and Thomas et al. (1979), which identified a ratio of 40% cover to 60% forage areas as an optimal mix of habitats for elk.

If timber harvest changes human access within and near the harvest units, elk distributions can be expected to shift, with elk avoiding areas with increased access, and selecting areas with little or no access (Wisdom and Cook 2000). Specifically, high road densities negatively influence elk distribution, in that elk avoid habitats near roads open to traffic (Rowland et al. 2000, Wisdom et al. 2004). The influence of open roads is not uniform, however, in that elk show increasing avoidance of areas near roads with increasing rates of motorized traffic (Wisdom et al. 2004). Cole et al. (1997) found that road management areas where access was restricted to administrative uses reduced home-range size and increased the survival of Roosevelt elk. Additionally, Lyon (1976) found that elk used habitats with greater canopy closure in areas of higher road density.

Timber harvest also affects the vulnerability of elk to hunting. Lyon and Christensen (1992:3) defined elk vulnerability as a "measure of elk susceptibility to being killed during the hunting season." Elk vulnerability to hunting can be affected by two aspects of timber harvest (Christensen et al. 1991). First, the removal of timber opens up the landscape, making elk more visible and therefore more vulnerable to harvest by hunters. And second, the increased number and extent of roads established to facilitate removal of logs greatly enhances the opportunity for more hunters to access the landscape, increasing the likelihood of hunter contact with elk. These effects were documented by Leptich and Zager (1991), Unsworth et al. (1993), and Hayes et al. (2002), and discussed at length in the compilation of papers by Christensen et al. (1991).

In contrast to elk, no major changes in cattle distribution during timber harvest are likely because domesticated animals typically are confined to pastures and generally tolerate human activities. Following timber harvest and the concomitant decrease in overstory canopy, however, a release of understory vegetation occurs that alters forage biomass, quality, and phenology, often leading to changes in cattle distribution. Forage biomass can increase from 2 to 8 times that of pre-harvest forage production (Svejcar and Vavra 1985) depending on intensity of the cut, site potential, and soil disturbance (Hedrick et al. 1968). Miller and Krueger (1976) reported that 60% of the forage consumed in a given pasture by cattle was from areas logged and reseeded. Road construction to facilitate harvest also provides improved distribution for cattle (Hedrick et al. 1968). Consequently, timber harvest generally provides new grazing areas for cattle.

Harris (1954) also reported that cattle seldom use dense overstory canopies except during conditions of extreme heat or intense insect harassment. Hedrick et al. (1968) found it more difficult to obtain moderate or heavy forage use by cattle under dense overstory canopies than under open canopies. Consequently, cattle distribution and use of new forage areas can be expected to increase substantially after timber harvest, until such time that overstory canopies again become dense.

Depending on season of use, livestock production may or may not be improved by timber harvest. Svejcar and Vavra (1985) found that forage quality on timber-harvested sites declined more rapidly than on unharvested sites. Consequently, weight gain per individual animal could actually decline in late summer on harvested sites. However, weight gain per acre could improve dramatically if stocking rates were increased to match the improvement in forage production in early and mid summer (Svejcar and Vavra 1985).

Timber Harvest Experiment at Starkey

Methods of Implementing the Timber Harvest Activities

We studied cattle and elk responses to timber harvest in the 3,590-acre (1,454 ha) Northeast Study Area of Starkey (Figure 1) from 1989-1996, encompassing periods before, during, and after harvest. The area is enclosed with an ungulate-proof fence, thus allowing direct measurements of ungulate responses to controlled, landscape experiments such as timber harvest, traffic, hunting, and other public land uses (Rowland et al. 1997, Wisdom et al. 2004). To study cattle and elk responses to our timber harvest experiment, a mosaic of units was harvested across the study area over a short time period, and no other human activities beyond those associated with timber management and hunting were allowed.

Timber sale planning and layout of harvest units occurred from 1989-1991, timber harvest and log hauling occurred during 1992, and conifer regeneration activities (site preparation, planting of tree seedlings, and stocking surveys) occurred from 1993-1996. Throughout our analyses and paper, we refer to the period of timber sale planning and layout as "before" harvest, the period of timber harvest and log hauling as "during" harvest, and the period of conifer regeneration activities as "after" harvest. Details about each period were described by Rowland et al. (1997)

Timber harvest during 1992 consisted of approximately 7 million board feet of commercial tree species that were logged from 1,207 acres (488 ha) of the study area from November 1991 through 1992 (referred to here as 1992 or "during" harvest period). Timber harvest encompassed 50% of forested lands in the Northeast Study Area (Figure 1). Harvest was a salvage sale that focused on removal of grand fir (Abies grandis) and Douglas-fir (Pseudotsuga menziesii) that had been killed by the combined effects of western spruce budworm (Choristoneura occidentalis), Douglas-fir tussock moth (Orgyia pseudotsugata), and drought during 1988-1990.

Most timber harvest took the form of shelterwood and seed tree regeneration cuts, with some commercial thinning and individual tree selections. The 63 harvest units ranged in size from 3 to 55 acres (1.2 to 22 ha). Harvest units were dispersed throughout the study area, denying ungulates the opportunity to find large areas of escape cover (Figure 1). Moreover, management guidelines for elk cover, such as maintenance of dense cover for presumed hiding and thermoregulatory benefits (Thomas et al. 1979, 1988), were intentionally ignored as part of the experimental design. Finally, the relatively small size of the study area (3,590 acres (1,454 ha)), smaller than many summer ranges used by elk (Leckenby 1984, Edge et al. 1985), combined with the ungulate fence, did not allow animals the option of avoiding the experiment by leaving the area or moving to locations far from harvest activities. Instead, the experiment was intentionally designed to measure cattle and elk responses to changes in the environment brought about by timber harvest, in the absence of options for ungulates to avoid the experimental area.

Extensive road construction also took place to facilitate log removal (Figure 1). Approximately 24 miles (39 km) of new roads were constructed. Another 4 of the 10 miles (6.5 of the 16 km) of roads present before timber harvest were renovated. The study area, however, was closed to public access, with the exception of hunting seasons each fall, when hunters were allowed entry for hunting purposes only (Rowland et al. 1997).

Despite no public entry, the study area received substantial road traffic in relation to timber sale planning and layout, timber harvest and log hauling, and conifer regeneration activities. Motorized traffic entering the study area during timber sale planning and layout (1989-1991) averaged 10 vehicles per day and was composed mostly of Forest Service vehicles and some vehicles associated with reconnaissance work by logging crews. During timber harvest and log hauling (1992), traffic entering the study area increased to an average of 29 vehicles per day; this traffic was composed almost entirely of log trucks, hauling logs from the harvest units, and minor traffic from logging crews and Forest Service contract administrators.

When harvest was completed (1993-1996), traffic entering the study area declined substantially to an average of 3 vehicles per day, composed mostly of Forest Service vehicles and some contractor's vehicles associated with conifer regeneration activities. An even lower rate of traffic (<1 vehicle per day) occurred during the hunting seasons each fall, from 1989-1995, when hunters were allowed vehicle entry only to retrieve game brought to roads. Traffic rate increased to >10 vehicles per day during hunting seasons in 1996, when vehicle access by hunters was allowed on established roads.

For all periods of study, estimates of traffic rate were based on automated traffic counters installed and monitored at or near the entry/exit point to the study area (Figure 1), using methods described by Rowland et al. (1997) and Wisdom et al. (2004). An automated, 16-millimeter camera also was installed and monitored at the entry/exit point (Rowland et al. 1997), which verified that traffic was dominated by Forest Service vehicles before harvest, by log trucks during harvest, and again by Forest Service vehicles after harvest.

Methods of Measuring Cattle and Elk Responses to Timber Harvest

We assessed the short-term effects of timber harvest on cattle and elk by evaluating their spatial distributions before (1989-1991), during (1992), and after (1993-1996) harvest. We also evaluated annual weight gains of each species before, during, and after harvest across those same years. Finally, we estimated the vulnerability of elk to hunting before, during, and after timber harvest. The experiment ended in 1996, and thus we did not measure long-term (>10 years post-harvest) responses of ungulates to timber harvest.

We maintained approximately 50 cow elk, their calves, and 12 adult bull elk in our study area each year, from spring through fall, throughout all periods of study. Elk entered the study area during early to mid-April of each year from an adjacent Winter Area (Rowland et al. 1997). By late fall (early to mid-December), elk typically were trapped and moved or baited from the study area back to the adjacent Winter Area (see Rowland et al. 1997). Winter 1991-1992 was extremely mild and we were unable to remove or entice many of the elk from the study area that winter, which reduced sample sizes of animals during 1991-1992 that were used to estimate spatial distributions with radio-telemetry (Table 1) and to estimate weight gains. We stocked 50 cow/calf pairs of cattle in the study area from mid-June through mid-October of each year as part of a season-long summer grazing system described by Rowland et al. (1997).

Estimating Changes in Cattle and Elk Distributions.

To estimate changes in spatial distributions of cattle and elk, we monitored the movements of radio-collared adult females of each species (Table 1) with an automated telemetry system described by Findholt et al. (1996, 2002), Rowland et al. (1997), and Kie et al. (2004). We used random samples consisting of 1,000 locations selected from the radio-collared animals that were monitored during each of the three periods (before, during, and after harvest, Table 1). Samples of locations therefore were a representative (random) composite taken from all radio-collared animals that were monitored in a given period.

We used the animal locations to estimate the distribution of each species during each period under a fixed-kernel analysis (Worton 1989). We used a bandwidth set at 0.5 of the reference bandwidth and plotted volume contours at increments of 0.05 from 0.05 to 0.95. Kernel methods provide a "probability density estimate of a distribution based on a sample of points" (Seaman et al. 1998:95). The kernel method of estimating and mapping distributions has been used extensively in wildlife research because it is a non-parametric estimator that requires few assumptions in contrast to parametric methods (Kernohan et al. 2001, Marzluff et al. 2001, 2004). Moreover, the kernel method is an unbiased estimator of the underlying, true animal distribution when a sufficient number (>300 locations) of unbiased animal locations are used (Garton et al. 2001).

We initially mapped the kernel distributions of animal locations, by the 0.05-contour intervals, for each species and time period in the study area. These maps provided an overall picture of spatial use by each species for each time period. For all subsequent analyses, we used the portion of each species' distribution occurring within the upper 50% of kernel volume, or 50% contour, for each time period. The upper 50% of kernel volume highlights areas of concentrated use by elk or cattle. Such areas often are referred to as "core areas" in analyses of spatial use (Kernohan et al. 2001). Throughout our paper, we refer to these areas as the "upper 50% of kernel volume", "50% core area", or "core area". These areas also are referred to as centers of a "utilization distribution," as described by Millspaugh et al. (2000) and Marzluff et al. (2001).

Because core areas or centers of utilization distributions are based on a substantially higher number of animal locations than the outer contours of such distributions, the core areas typically provide a more robust estimate in contrast to estimates made at the periphery of the kernel volume (Seaman et al. 1998, 1999, Marzluff et al. 2001). Moreover, our interest was in monitoring changes in concentrated areas of use (the most frequently used areas) across time periods, as could be done with analysis of the core areas.

We used maps of the upper 50% of kernel volume to estimate the change in spatial use by cattle and elk in four ways. First, we calculated the percent area within the upper 50% of kernel volume for each species and time period that occurred in each of four regions, or quadrants, in our study area. For this analysis, we subdivided the study area into northwest, northeast, southwest, and southeast quadrants, each of equal size. We then expressed the percent area of the upper 50% of kernel volume occurring within each of the quadrants as a percentage, for each species and time period. This analysis allowed us to further quantify the shift in species' distributions across periods. Millspaugh et al. (2000) employed similar concepts in their application of utilization distributions for assessing hunter-elk interactions.

Second, we calculated the percent overlap of the cut units (top right, Figure 1) within the upper 50% of kernel volume, by species and time period. This analysis was intended to portray the degree to which cattle or elk distributions may have shifted away from or toward the harvest units during or after harvest. For example, if percent overlap of the harvest units with the upper 50% of kernel volume was 70% before timber harvest but 35% during harvest, this would suggest the species was avoiding the units during harvest activities.

Third, we calculated the percent area within the 50% core area for each species and time period across the entire study area. Under this analysis, if a higher percentage of the study area occurred under the core area, this would indicate that distributions of cattle or elk were more diffuse, or spread out, across a larger area. A lower percentage would indicate that distributions were more concentrated in smaller portions of the study area. The degree to which distributions are more diffuse or concentrated has been used as an index of habitat quality in home-range analyses. Larger core areas or home ranges suggest lower habitat quality, whereas smaller areas indicate higher habitat quality, owing to like differences in the area over which animals must meet their needs (e.g., see Carey et al. 1992, Zabel et al. 1995, Cole et al. 1997).

Fourth, we assessed the degree to which cattle and elk selected or avoided the mainline roads, which received highest frequency of motorized traffic (N. Cimon, unpublished data, 2004) that entered the study area (see traffic rates stated earlier). Mainline roads were identified as the 400, 430, and 480 roads before harvest (top left, Figure 1), and the 400, 420, 430, 437, 440, 460, and 480 roads during and after harvest (top right, Figure 1). For this analysis, we calculated the mean distance of 30- x 30-meter pixels to the closest mainline road, for those pixels within each species' core area during each period; this constituted our estimate of the area used by each species in relation to distance from the mainline roads. We then divided this number by the mean distance of the entire study area's 30- x 30-meter pixels (n = 16,133) to the closest mainline road, which constituted our estimate of the area available to each species in relation to distance from the mainline roads. A ratio of 1.0 of used versus available pixels suggests neither selection nor avoidance of roads. A ratio >1.0 indicates avoidance; a ratio <1.0 suggests selection toward roads.

We also calculated the mean percent slope and mean percent overhead canopy closure of all 30-x 30-meter pixels within the species' 50% core for each time period, and compared these estimates across time and with overall estimates for the study area. We did this to gain further insight as to whether ungulates might have been seeking areas of greater security (Christensen et al. 1991) in proximity to roads or cut units during and after harvest. These variables were available from spatial layers estimated and used in prior ungulate research at Starkey (Johnson et al. 2000, Rowland et al. 2000).

A minor effect on our distribution analyses resulted from our not restricting the kernel estimation to the specific boundaries of the study area. That is, elk and cattle movements were restricted to the enclosure boundaries that formed our study area (Figure 1), but kernel estimation was not. This resulted in a small portion of kernel volume being mapped along or just outside the study area boundaries. Consequently, the core areas used in our analyses would have changed slightly if we had constrained the kernel estimation to the specific enclosure boundaries.

Estimating Changes in Weight Gains of Cattle and Elk.

To evaluate potential effects of changes in nutritional status of ungulates following timber harvest, we estimated annual weight gains of each species, and compared these annual changes over time. To account for annual variation in ungulate weight gains due to annual differences in weather and associated forage conditions, we also calculated weight gains for cattle and elk in the Main Study Area of Starkey (Figure 1) as a background reference for conditions of no timber harvest. The Main Study Area is immediately adjacent to the Northeast Study Area, is subject to the same weather conditions, and was not subjected to timber harvest activities during the period of our study (1989 through 1996) (See Rowland et al 1997 for details). Thus, we used the weight gains from the Main Study Area as a control, against which changes in ungulate weight gains in the Northeast Study Area could be compared.

To estimate annual weight gain, we weighed adult cow elk (>2 yrs old) during late winter or early spring (late February to early April) before animals entered each study area, and during late fall or early winter (late November to early January) after these same animals left that study area. We weighed calf elk after they left the study areas in early winter. Similarly, we weighed adult cattle (>2 yrs old) and calves as they entered the study areas in mid-June and as they left the study areas in mid-October of each year.

Annual weight gains were expressed as an average daily gain for elk cows and for beef cows and calves. Specifically, we computed the difference between each animal's weight before it entered the study area and the weight after it left. We divided that difference by the number of days over which the difference was computed. We then calculated a mean daily gain and 95% confidence interval about the mean for each species and age class for each year.

Standardizing each animal's weight gain by the number of days over which the gain was measured accounted for the fact that some animals were weighed earlier or later than other animals before entering or after leaving the study areas. Only elk cows and beef cows and calves with weights measured both before entering the study areas, and after leaving the study areas, were included in our analysis of a given year's weight gains. Thus, we used a repeated measures approach in calculating weight gains, in that gains were computed for each animal, based on its weight before entering and after leaving the study area, which increased the precision of our estimates.

For elk calves, all of which were born in the study areas, we calculated the weight gain in absolute amount for each animal, based on their fall weights after they left the study area. We calculated a mean weight of elk calves, and 95% confidence interval about the mean, for each year and study area.

Under our analysis, if timber harvest did not affect weight gains, we would expect that variation in gains observed in our study area would remain consistent with gains calculated for these species and age classes each year in the Main Study Area, and that annual variation in gains in both study areas was due to variation in weather or other factors. By contrast, if timber harvest caused an increase or decline in weight gains, we would expect gains in our study area to increase or decrease in relation to such gains observed for the same species and age class in the Main Study Area.

Monitoring Changes in Elk Vulnerability to Hunting.

We evaluated the vulnerability of elk to being killed by hunters before, during, and after timber harvest with data from hunts of branch-antlered bulls that occurred in the study area from 1989 through 1996 (Rowland et al. 1997). For each year, we calculated hunter success rates and the number of days required for hunters to harvest an animal, using information from Starkey's hunter check station (Rowland et al. 1997). From 1990 through 1995, the branch-antlered bull hunt was foot-access only, with permission to use vehicles to retrieve dead animals. In 1996, vehicle access during the hunting season was allowed. Under this analysis, if hunter success increased or the number of days required to kill an elk decreased during or after timber harvest, this would suggest that the increased openness and road access resulting from timber harvest caused elk to be more vulnerable to hunting.

Changes in Cattle and Elk Distributions

Before timber harvest (1989-1991), elk were concentrated in the western portion of the Northeast Study Area (Figure 2), particularly in the southwest quadrant (Figure 3). Elk distribution shifted substantially during timber harvest (1992) with use concentrated along portions of the study area's outer boundaries (Figure 2). Elk distribution shifted most to the southeast and northeast quadrants during harvest, which had received little use beforehand (top right, Figure 3). Elk distributions also became more diffuse during timber harvest. Nearly twice as much of the study area was within the upper 50% of kernel volume compared to the period before harvest (bottom right, Figure 3).

Distribution shifts by elk during harvest were not related to elk avoidance of the cut units, as areas where timber cutting occurred overlapped more with the 50% core area for elk during harvest than before harvest (bottom left, Figure 3). Distribution shifts by elk during timber harvest also were not related to elk avoidance of the mainline roads used most frequently by log trucks (400, 420, 430, 437, 440, 460, and 480 roads, Figure 1)--the 50% core area for elk during harvest was closer to these roads than overall habitat available to elk. Specifically, the mean distance of all pixels in the 50% core area for elk was 655 yards (599 m) from these roads, but the overall area available to animals had a mean distance of 916 yards (838 m) to the same roads, for a selection ratio of 0.72 during harvest. Elk selection toward roads, however, was even stronger before harvest, when the selection ratio was 0.42, indicating that elk decreased their use near roads during harvest when traffic rate increased substantially (per traffic rates stated in methods).

In addition, the 50% core area for elk had a steeper average slope (21%) during harvest compared to the average slope (17%), suggesting that elk selected areas of greater security while close to roads. By contrast, the core area for elk had an average slope of 16% before harvest, similar to the average slope of 17% available to animals. Contrary to the pattern of elk seeking steeper slopes during timber harvest, the core area for elk had a mean overhead canopy closure (33%) similar to its availability (32%). This also was the pattern before harvest, when the core area for elk had a mean overhead canopy closure of 40% compared to available canopy closure of 41%.

In 1993-1996, after timber harvest was completed, elk again concentrated in the western half of the study area, as well as in the interior portions of the study area that were largely unused during timber harvest (Figure 2). As with the period before harvest, elk use was concentrated in the southwest quadrant (top right, Figure 3). Elk use of the southeast quadrant also diminished substantially, as occurred during harvest. Elk distribution also was more diffuse after timber harvest as compared to before harvest, but not as diffuse as during harvest (bottom right, Figure 3).

After timber harvest, elk also continued to select areas closer to the mainline roads than the area available for use. The mean distance of pixels in the 50% core area for elk was 332 yards (304 m) from these roads, but overall habitat available to animals had a mean distance of 916 yards (838 m) to the same roads, for a selection ratio of 0.36 after harvest. This selection ratio was twice as strong as that observed during harvest (0.72), further suggesting that elk moved closer to roads after log hauling was completed and traffic subsided (per traffic rates stated in methods). The average slope of pixels within the 50% core area for elk after harvest (17%) also was similar to that before harvest (16%), indicating that elk moved back to more gentle slopes once timber harvest had ended.

In contrast to elk, cattle showed little change in distribution during all periods of study (Figures 2, 3). The areas of highest concentration were generally consistent before, during, and after timber harvest, with little change in the percentage of the upper 50% of kernel volume by quadrant across time (top right,

Figure 3) or across the study area (bottom right, Figure 3). Harvest unit overlap with the 50% core area of cattle remained consistently between 20%-25% across all three periods (bottom left, Figure 3). The focal point of cattle distribution was along the Syrup Creek drainage (the east-west continuum of uncut area running east-west through the middle of the study area between the 420 and 480 roads, top right, Figure 1), coinciding with darkest areas of cattle use during all three periods in Figure 2. Interestingly, overlap of the cut units with the 50% core area for cattle was less than that for elk, both during and after timber harvest (bottom left, Figure 3), as was the percent area under the 50% core for cattle versus elk during these two periods (bottom left, Figure 3).

Cattle distributions, like those of elk, were consistently closer to the mainline roads than available habitat. The mean distance of pixels in the 50% core area for cattle was 1052 yards (962 m) from these roads, but overall habitat available to animals had a mean distance of 1206 yards (1103 m) to the same roads, for a selection ratio of 0.87 before harvest. The 50% core area for cattle was progressively closer to the mainline roads during and after harvest, with road selection ratios of 0.69 and 0.35, respectively.

Unlike elk, cattle showed no evidence of selection of areas with characteristics of greater security from humans. Average slopes under the core area used by cattle did not appear to change across time periods (before-17%; during-18%; after-16%) and was the same or similar to the average slope of 17% in the study area. Moreover, average overhead canopy closure of pixels in the core areas of cattle was highest before harvest (43%) but declined during and after harvest (34% for both periods), a pattern that corresponded to the change in average overhead canopy closure for the study area (42% before harvest, 32% during and after harvest).

Changes in Weight Gains of Elk and Cattle

Annual weights gains of adult female elk and calf elk in the Northeast Study Area were not different from gains for these same age classes in the Main Study Area, based on overlapping 95% confidence intervals between mean gains within each year and age class (Figure 4). Moreover, no trend in weight gains in either study area was evident (Figure 4). Instead, weight gains of elk cows and calves were highly variable across years in the Northeast Study Area, but consistent with the variability in weight gains observed across years in the Main Study Area, where timber harvest did not occur (Figure 4). That is, the direction and degree of variability in annual weight gains was generally consistent between the two study areas, suggesting that weight gains in elk were largely affected by annual variability in weather patterns that affect annual changes in forage biomass and quality (see Management Implications).

In contrast to elk, mean weight gains for beef cows and calves in the Northeast Study Area were mostly higher (non-overlapping 95% confidence intervals) than those documented in the Main Study Area within each year and age class (Figure 5). In 1992 and 1993, however, the 95% confidence intervals overlapped between mean weight gains of beef cows in the two study areas; and in 1995, mean weight gain of beef cows was higher in the Main Study Area (Figure 5). The pattern of higher weight gains in Northeast Study Area versus those in Main Study Area was more consistent for beef calves, except for one year (1992) where confidence intervals overlapped.

As with elk, no trend in weight gains in either study area was evident for either age class of cattle (Figure 5). Also similar to elk was the high annual variability in weight gain observed for beef cows and calves, and the strong consistency in the degree and direction of this variability between Main and Northeast Study Areas across years (Figure 5). In contrast to elk, however, cattle weight gains were more precise for each year, and the annual variability appeared to be more similar between the two study areas (compare Figure 4 with Figure 5).

Changes in Elk Vulnerability to Hunter Harvest

Compared to the period before timber harvest, hunter success improved and the number of hunter days per harvested animal declined during and after timber harvest (Table 2). The highest hunter success and the lowest number of hunting days required to take an animal occurred in 1996, when post-harvest, open conditions existed together with unlimited vehicle access (Table 2).

For the years before timber harvest (1989-1991), hunter success averaged 22%, requiring an average of approximately 19 days to achieve this level of success. During timber harvest (1992), hunter success increased to 35%, with hunters spending an average of approximately 9 days to achieve this success (number of days required to harvest an animal). For the years after timber harvest (1993-1996), hunter success remained higher and similar to success during the year of timber harvest, with an average success of 32%. Moreover, an average of 14 days were required for hunters to take an animal post-harvest.

Management Implications

Elk responded to the period of timber harvest by making a substantial shift in distribution, while cattle did not. Interestingly, the shift in distribution by elk, and the lack of change in distribution by cattle, did not appear to change animal performance for either species. Our study is one of the few cases in which a measure of animal or nutritional performance (weight gain) was evaluated in combination with distributional responses of animals under a landscape experiment. Garton et al. (2001) strongly emphasized the need to evaluate the population or nutritional consequences of landscape choices made by wildlife under studies of resource selection, habitat use, and spatial distribution. Garton et al. (2001) highlighted the few studies where the demographic or nutritional consequences of landscape choices made by a wildlife species were documented, and particularly noted that changes in animal selection or distribution do not always result in changes in population or animal performance.

In our study, the nutritional consequences of each species' spatial response to timber harvest suggest that each species' was able to maintain animal performance during and after harvest. And yet, one species (elk) substantially changed their distribution during the experiment, while the other species (cattle) did not. These results serve as a demonstration that studies of animal behavior and distribution in relation to human disturbances may not provide strong inference about demographic or nutritional effects.

Our results must be viewed with caution, however, as the relatively small sample sizes on which weight gains were estimated suggests that we had low statistical power and a higher likelihood of committing Type II errors; that is, of falsely concluding that weight gains did not change in relation to timber harvest when in fact such changes did occur, but were not detected. Moreover, we did not evaluate the long-term (>10 years post-harvest) effects of timber harvest on weight gains, which could be substantially different than short-term weight gains.

The substantial increase in percent area under the upper 50% of kernel volume for elk during and after timber harvest also serves as a cautionary note. This finding indicates that the elk population became more dispersed during and after timber harvest, suggesting longer movements over larger areas by elk to meet their needs. Larger areas used by a species indicate lower habitat quality and reduced population performance when these patterns exist over extended periods (e.g., see Carey et al. 1992, Zabel et al. 1995).

We also did not assess other response variables related to animal and nutritional performance of ungulates, such as those studied and discussed by Cook (2002) and Cook et al. (2004). Examples include estimates of pregnancy rates and body fat, which provide complementary insights on ungulate performance beyond measures of weight gain. Moreover, we did not evaluate changes in forage biomass, quality, and phenology that could have provided additional insights about changes in potential carrying capacity. We also did not assess diet selection or diet quality of ungulates, which provide direct estimates of the nutritional plane of animals (Cook 2002, Cook et al. 2004). Density of both species in the study area may have been low enough that weight gains for both species were high before timber harvest, and therefore did not change substantially following the presumed change in forage conditions after harvest.

Results from our analysis of cattle and elk distributions complement an earlier analysis of ungulates in our study area by Stewart et al. (2002), who found that cattle and elk were spatially separated during summer. Our results demonstrated a substantial shift in elk distributions during timber harvest, while cattle distributions were nearly unchanged. Our results therefore indicate that elk were responding more strongly to timber harvest activities than to cattle distributions.

Our results also are surprising in that we found no evidence that elk avoided the cut units or the mainline roads during and after timber harvest. The mainline roads received a high frequency of log-truck traffic throughout the harvest period of 1992, and it is possible that elk became habituated to this form of predictable, consistent traffic. This is in contrast to the less predictable and diverse forms of motorized traffic that occur when roads are open to the public, and that presumably contribute to elk avoidance of these open roads (e.g., Rowland et al. 2004, Wisdom et al. 2004). Importantly, our study area was not open to public access and motorized traffic, with the exception of highly restricted public traffic that was allowed as part of timber harvest and elk hunting. Model predictions of elk avoidance of roads open to traffic (e.g., Thomas et al. 1979, Rowland et al. 2000, 2004) do not account for specialized, restricted forms of high-frequency traffic such as that associated with timber harvest in areas that otherwise are closed to public access. This aspect of elk response to motorized traffic deserves more attention in future research.

Our results on weight gain for elk also complement an earlier analysis by Rinehart (2001), who found no difference in early winter weights of elk before versus after timber harvest in our study area. Rinehart (2001) also found no difference between annual weights of elk in our study and those in the adjacent, Main Study Area where timber harvest did not occur. Finally, Rinehart (2001) also noted that changes in resource selection and home-range size after timber harvest did not equate to a reduction in animal performance of elk, as indicated by the lack of a trend in early winter weights before versus after harvest.

The high variability in weight gains across years for both ungulate species and all age classes strongly suggests that annual gains were largely affected by annual variability in weather patterns that affect annual changes in forage biomass and quality. This suggestion is supported by work of Vavra and Phillips (1979, 1980), who found that variation in summer precipitation directly affected the diet quality and subsequent weight gains of cattle on northeast Oregon summer ranges having similar weather and forage conditions as those in our study area. During a drought year (1977), diet quality of cattle was substantially lower than years of higher summer moisture (1975 and 1976), resulting in substantially lower weight gains during the drought year.

These patterns of high variability in weight gains of domestic ungulates in response to year-to-year variation in weather, precipitation, and subsequent forage conditions were summarized by Holechek et al. (1989, 1998); these authors concluded that growing season variability in precipitation exerted a strong effect on ungulate performance on rangelands across the western United States, particularly during drought years. Similar inferences were made by Cook et al. (2002) regarding annual variation in elk performance, as affected by annual variation in summer weather that appears to have a strong influence on summer nutrition of animals.

Although animal performance of elk did not appear to change in response to timber harvest, the post-harvest landscape in our study area clearly increased hunter success and reduced the number of hunting days required to harvest an animal. These results suggest that increased visibility and access associated with timber harvest increased the vulnerability of elk to being killed by hunters. These results further suggest that timber harvest may have the strongest and most enduring effects on elk vulnerability to hunting, in contrast to other effects we measured such as changes in distribution and potential avoidance of human disturbances. Consequently, our results suggest that the potential for intensive timber harvest to substantially increase elk vulnerability to hunting is a key issue that deserves careful attention as part of timber harvest planning.

Those points as context, consideration of our results, combined with results from previous studies (see “Overview of Current Knowledge”), could focus on timber sale designs that minimize elk vulnerability to hunting and that provide a relatively even and continuous stream of forage availability over space and time. Example considerations at the watershed scale could include the following:

- Manage for and retain security areas for elk in watersheds when planning the layout of harvest units in time and space. Security areas serve primarily to mitigate any increase in elk vulnerability to hunting when timber harvest activities result in increased visibility and human access in a watershed. A security area for elk was defined by Hillis et al. (1991:38) as a nonlinear block of hiding cover at least 250 acres (101 ha) in size and at least one-half mile (0.8 km) from roads open to motorized traffic. Hiding cover was defined by Thomas et al. (1979:109) as vegetation capable of hiding 90% of a standing adult deer or elk from the view of a human at a distance equal to or less than 200 feet (61 m). In particular, Hillis et al. suggested that security areas are most effective in minimizing elk vulnerability to hunting when such areas compose at least 30% of a watershed. However, other management options, such as minimizing road access, accounting for elk security provided by steep slopes and convex topography, and changes in hunting season regulations, also can be considered in tandem with management of security areas. These additional management options were outlined and discussed by Thomas (1991).
- Restrict motorized and mechanized forms of hunter access in watersheds after timber harvest, to prevent an increase in elk vulnerability to harvest by hunters. Maintain such restrictions on motorized and mechanized forms of hunter access until such time that vegetative growth in timber harvest units provides sufficient hiding cover to help reduce vulnerability. In watersheds with flat terrain and large areas subjected to timber harvest over a short time period, restrictions on human access will be especially effective in minimizing an increase in elk vulnerability to hunting. In watersheds with steep terrain and large areas of hiding cover, restrictions on hunter access after timber harvest may be neither necessary nor effective, in that elk may have ample areas in which to hide or find security from hunters. In particular, plan the layout of harvest units to retain security areas (particularly areas with steeper slopes and greater convexity) near the cut units to facilitate animal escapement from these focal points of hunter access (per discussion by Hillis et al. 1991).
- Plan timber harvest activities in time and space such that a mosaic of seral stages are maintained to provide a variety of foraging conditions for cattle and elk. Timber harvest is likely to cause an immediate but short-term (1-3 year) decline in forage availability in the harvest units, followed by a large increase in forage that may last 10 years or longer. The biomass and phenology of forage plants is likely to be more diverse and stable with the implementation of a mosaic of timber harvest activities in time and space. Security areas for elk can also be sustained consistently under a strategy of timber harvest that produces a mosaic of seral stages in time and space.
-

Acknowledgments

We thank B. Dick, M. Rowland, and S. Findholt for reviewing our paper, and B. Naylor for help with analysis and mapping. L. Bryant and J. Thomas initiated the study and obtained funding and logistical support for the research. Funding and in-kind support was provided by Boise Cascade Corporation, Oregon Department of Fish and Wildlife, U.S. Department of Interior Fish and Wildlife Service Federal Aid for Wildlife Restoration, and the Pacific Northwest Region and Pacific Northwest Research Station of U.S. Department of Agriculture Forest Service.

Literature Cited

Black, H., R. J. Scherzinger, and J. W. Thomas. 1976. Relationships of Rocky Mountain Elk and Rocky Mountain Mule Deer habitat to timber management in the Blue Mountains of Oregon and Washington. In *Proceedings, Elk-logging-roads symposium,* 11-31. Moscow: University of Idaho.

Boyce, M. S., M. G. Turner, J. Fryxell, and P. Turchin. 2002. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10:421-431.

Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs* 62:223-250.

Christensen, A. G., L. J. Lyon, and T. N. Lonner, compilers. 1991. *Proceedings, Elk Vulnerability Symposium*, 1-330. Bozeman, Montana State University.

Cole, E. K., M. D. Pope, and R. G. Anthony. 1997. Effects of road management on movement and survival of Roosevelt elk. *Journal of Wildlife Management* 61:1115-1126.

Cook, J. G. 2002. Nutrition and food. In D. E. Toweill and J. W. Thomas, eds, *North American elk: ecology and management*, 259-349. Washington, D.C. Smithsonian Institution Press.

Cook, J. G., B. K. Johnson, R. C. Cook, R A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* 155:1-61.

Crouch, G. L. 1974. Interaction of deer and forest succession on clearcuttings in the Coast Range of Oregon. In Black, Hugh C. ed, *Proceedings, wildlife and forest management in the Pacific Northwest*, 133-138. Corvallis, Oregon State University.

Edge, W. D., and C. L. Marcum. 1985. Movements of elk in relation to logging disturbances. *Journal of Wildlife Management* 49(4):926-930.

Edge, W. D., and C. L. Marcum. 1991. Topography ameliorates the effects of roads and human disturbance on elk. In A. G. Christensen, L. J. Lyon, and T. N. Lonner, compilers, *Proceedings, Elk Vulnerability Symposium*, 132-137. Bozeman, Montana State University.

Edge, W. D., C. L. Marcum, and S. L. Olson. 1985. Effects of logging activities on home-range fidelity of elk. *Journal of Wildlife Management* 49(3):741-744.

Findholt, S. L., B. K. Johnson, L. D. Bryant, and J. W. Thomas. 1996. Corrections for position bias of a LORAN-C radio-telemetry system using DGPS. *Northwest Science* 70:273-280.

Findholt, S. L., B. K. Johnson, J. W. Kern, A. A. Ager, L. L. McDonald, and R. J. Stussy. 2002. *Adjusting for radiotelemetry error to improve estimates of habitat use*. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-555, Portland, Oregon.

Garton, E. O., M. J. Wisdom, F. A. Leban, and B. K. Johnson. 2001. Experimental design for radiotelemetry studies. In J. Millspaugh and J. Marzluff, eds., *Radio tracking and animal populations*, 1-42. Sand Diego, Academic Press, CA.

Gutzwiller, K. J., editor. 2002. *Applying landscape ecology in biological conservation*. New York, Springer-Verlag.

Hayes, S. G., D. J. Leptich, and P. Zager. 2002. Proximate factors affecting male elk hunting mortality in northern Idaho. *Journal of Wildlife Management* 66:491-499.

Harris, R. W. 1954. Fluctuations in forage utilization of ponderosa pine range in eastern Oregon. *Journal of Range Management* 7:250-255.

Hedrick, D. W., J. A. Young, J. A. B. McArthur, and R. F. Kenniston. 1968. *Effects of forest and grazing practices on mixed coniferous forests in northeastern Oregon*. Agricultural Experimental Station, Technical Bulletin 103. Corvallis, Oregon State University.

Hershey, T. J., and T. A. Leege. 1976. Influences of logging on elk on summer range in north-central Idaho. In *Proceedings, Elk-logging-roads symposium*, 73-80. Moscown, University of Idaho.

Hillis, J. M., M. J. Thompson, J. E. Canfield, L. J. Lyon, C. L. Marcum, P. M. Dolan, and D. W. McCleerey. 1991. Defining elk security: the Hillis paradigm. In A. G. Christensen, L. J. Lyon, and T. N. Lonner, compilers, *Proceedings, Elk Vulnerability Symposium*, 38-43. Bozeman, Montana State University.

Holechek, J.L., R.D. Pieper, and C.H. Herbel. 1989. *Range management principles and practices*, second edition. Prentice-Hall, Englewood Cliffs, NJ.

Holechek, J.L., R.D. Pieper, and C.H. Herbel. 1998. *Range mangement principles and practices*, third edition. Prentice-Hall, Englewood Cliffs, NJ.

Johnson, B. K, J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk in spring. *Journal of Wildlife Management* 64:685-697.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. In J. Millspaugh and J. Marzluff, eds., *Radio tracking and animal populations*, 126-166. San Diego, Academic Press, CA.

Kie, J. G., A. A. Ager, N. J. Cimon, M. J. Wisdom, M. M. Rowland, P. K. Coe, S. L. Findholt, B. K. Johnson, and M. Vavra. 2004. The Starkey Database: Spatial-environmental relations of North American elk, mule deer, and cattle at the Starkey Experimental Forest and Range in Northeastern Oregon. *Transactions of the North American Wildlife and Natural Resources Conference* 69: 475-490.

Leckenby, D. A. 1984. *Elk use and availability of cover and forage habitat components in the Blue Mountains, northeast Oregon, 1976-1982*. Wildlife Research Report Number 14, Oregon Department of Fish and Wildlife, Portland, Oregon.

Leege, T. A. 1976. Relationship of logging to decline of Pete King Elk herd. In *Proceedings, Elk-logging-roads symposium*, 6-10. Moscow, University of Idaho.

Leptich, D. J., and P. Zager. 1991. Road access management effects on elk mortality and population dynamics.In A. G. Christensen, L. J. Lyon, and T. N. Lonner, compilers, *Proceedings, Elk Vulnerability Symposium*, 126-137. Bozeman, Montana State University.

Lyon, L. J. 1976. Elk use as related to characteristics of clearcuts in western Montana. In *Proceedings, Elk-logging-roads symposium*, 69-72. Moscow, University of Idaho.

Lyon, L.J. 1979. *Influences of logging and weather on elk distribution in western Montana*. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. Research Paper INT-RP-236, Ogden, Utah.

Lyon, J. L., and A. G. Christensen. 1992. *A partial glossary of elk management terms*. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station INT-GTR-288, Ogden, Utah.

Lyon, L. J., and A. G. Christensen. 2002. Elk and land management. In D. E. Toweill and J. W. Thomas eds., *North American Elk Ecology and Management*, 557-582. Washington D.C., Smithsonian Institution Press.

Lyon, L. J., and C. E. Jensen. 1980. Management implications of elk and deer use of clear-cuts in Montana. *Journal of Wildlife Management* 44(2):352-362.

Marzluff, J. M., S. T. Knick, and J. J. Millspaugh. 2001. High-tech behavioral ecology: modeling the distribution of animal activities to better understand wildlife space use and resource selection. In J. Millspaugh and J. Marzluff, eds., *Radio tracking and animal populations*, 310-326. San Diego, Academic Press, CA.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: Forest fragments and Steller's jays. *Ecology* 85:1411–1427.

Miller, R. F., and W. C. Kruerger. 1976. Cattle use on summer foothill rangelands in northeastern Oregon. *Journal of Range Management* 29:367-371.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing in South Dakota. *Journal of Wildlife Management* 64(4):994-1003.

Parker, K. L. 2002. Advances in nutritional ecology of cervids at different scales. *Ecoscience* 10:395-411.

Perry, C., and R. Overly. 1976. Impact of roads on big game distribution in portions of the Blue Mountains of Washington. In *Proceedings, Elk-logging-roads symposium*, 62-68. Moscow, University of Idaho.

Reynolds, H. G. 1966. *Use of openings in spruce-fir forests by deer, elk, and cattle*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station Research Note RM-RN-63, Ft. Collins, Colorado.

Rinehart, J. M. 2001. Effects of intensive salvage logging on Rocky Mountain elk at the Starkey Experimental Forest and Range. M.S. Thesis, University of Montana, Missoula.

Rowland, M. M., L. D. Bryant, B. K. Johnson, J. H. Noyes, M. J. Wisdom, and J. W. Thomas. 1997. *The Starkey project: History, facilities, and data collection methods for ungulate research*. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-396, Portland, Oregon.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. *Journal of Wildlife Management* 64(3):672-684.

Schroer, G. L., K. J. Jenkins, B. B. Moorhead. 1993. Roosevelt elk selection of temperate rain forest seral stages in western Washington. *Northwest Science* 67(1):23-29.

Scott V. E., G. L. Crouch, and J. A. Whelan. 1982. *Responses of birds and small mammals to clearcutting in a subalpine forest in Central Colorado*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Station, Research Note RM-RN-422, Ft. Collins, Colorado.

Seaman, D. E., B. Griffith, and R. A. Powell. 1998. KERNELHR: a program for estimating animal home ranges. *Wildlife Society Bulletin* 26: 95-100.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63(2): 139-147.

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: Resource partitioning and competitive displacement. *Journal of Mammalogy* 83:229-244.

Svejcar, T., and M. Vavra. 1985. The influence of several range improvements on estimated carrying capacity and potential beef production. *Journal of Range Management* 38:395-399.

Thomas, J. W., H. Black, Jr., R. J. Scherzinger, and R. J. Pedersen. 1979. Deer and elk. In *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington,* ed. J. W. Thomas, 104-127. U.S. Department of Agriculture, Forest Service, Agricultural Handbook No. 553. Portland, Oregon.

Thomas, J. W., D. A. Leckenby, M. Henjum, R. J. Pedersen, and L. D. Bryant. 1988. *Habitat-effectiveness index for elk on Blue Mountain winter ranges*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, PNW-GTR-218. Portland, Oregon.

Thomas, J. W. 1991. Elk vulnerability – a conference perspective. In A.G. Christensen, L.J. Lyon, and T.N. Lonner, compilers, *Proceedings, Elk Vulnerability Symposium*, 318-319.Bozeman, Montana State University.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. *Landscape ecology in theory and practice, pattern and process*. New York, Springer-Verlag.

Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the Clearwater drainage of northcentral Idaho. *Journal of Wildlife Management* 57(3):495-502.

Unsworth, J. W., L. Kuck, E. O. Garton, and B. R. Butterfield. 1998. Elk habitat selection on the Clearwater National Forest, Idaho. *Journal of Wildlife Management* 62:1255-1263.

Vavra, M., and R. L. Phillips. 1979. Diet quality and cattle performance on forested rangeland in northeastern Oregon. *Proceedings, Western Section, American Society of Animal Science* 30:170-173.

Vavra, M., and R. L. Phillips. 1980. Drought effects on cattle performance. *Proceedings, Western Section, American Society of Animal Science* 31:157-160.

Ward, A. L. 1976. Elk behavior in relation to timber harvest operations and traffic on the Medicine Bow Range in South-Central Wyoming. In *Elk-logging-roads symposium proceedings*, 32-57. Moscow, University of Idaho.

Wisdom, M. J., L. R. Bright, C. G. Carey, W. W. Hines, R. J. Pedersen, D. A. Smithey, J. W. Thomas, and G. W. Witmer. 1986. *A model to evaluate elk habitat in western Oregon*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Publication No. R6-F&WL-216-1986, Portland, Oregon.

Wisdom, M. J., and J. W. Thomas. 1996. Elk. In *Rangeland Wildlife,* ed. P.R. Krausman, 157-182. Denver: Society for Range Management, Colorado.

Wisdom, M. J., and J. G. Cook. 2000. North American elk. In *Ecology and management of large mammals in North America,* eds. S. Demarais and P. R. Krausman, 694-735. Upper Saddle River, New Jersey, Prentice-Hall, Inc.

Wisdom, M. J., N. J. Cimon, B. K. Johnson, E. O. Garton, and J. W. Thomas. 2004. Spatial partitioning by mule deer and elk in relation to traffic. *Transactions of the North American Wildlife and Natural Resources Conference* 69:509-530.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.

Zabel, C. J., K. McKelvey, and J. P. Ward, Jr. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (Strix occidentalis caurina). *Canadian Journal of Zoology* 73(3):433-439.

Table 1. Number of radio-collared elk and cattle for each year before (1989-1991), during (1992), and after (1993-1996) timber harvest in the Northeast Study Area of Starkey Experimental Forest and Range, northeast Oregon.

Year	**No. Elk**	**No. Cattle**
1989	10	9
1990	18	15
1991	11	13
1992	4	12
1993	12	11
1994	20	13
1995	13	9
1996	13	10

Table 2. Success rates and number of days hunted by elk hunters during branch-antlered bull hunts that occurred before (1989-1991), during (1992), and after (1993-1996) timber harvest in Northeast Study Area, Starkey Experimental Forest and Range. Data on number of days hunted and number of days hunted per animal harvested were not available (na) for 1989.

Year	No. Hunters	No. Elk Harvest	No. Days Hunted	Hunter Success (percent)	No. Days Hunted per Animal Harvested	No. Animals Available for Harvest	Type of Hunter Access Allowed
1989	10	3	na	30	na	6	foot only
1990	23	5	127	22	25.4	10	foot only
1991	14	2	63	14	31.5	8	foot only
1992	26	9	78	35	8.7	13	foot only
1993	15	3	66	20	22.0	10	foot only
1994	27	5	95	19	19.0	12	foot only
1995	23	8	81	35	10.1	12	foot only
1996	24	13	69	54	5.3	14	vehicle access

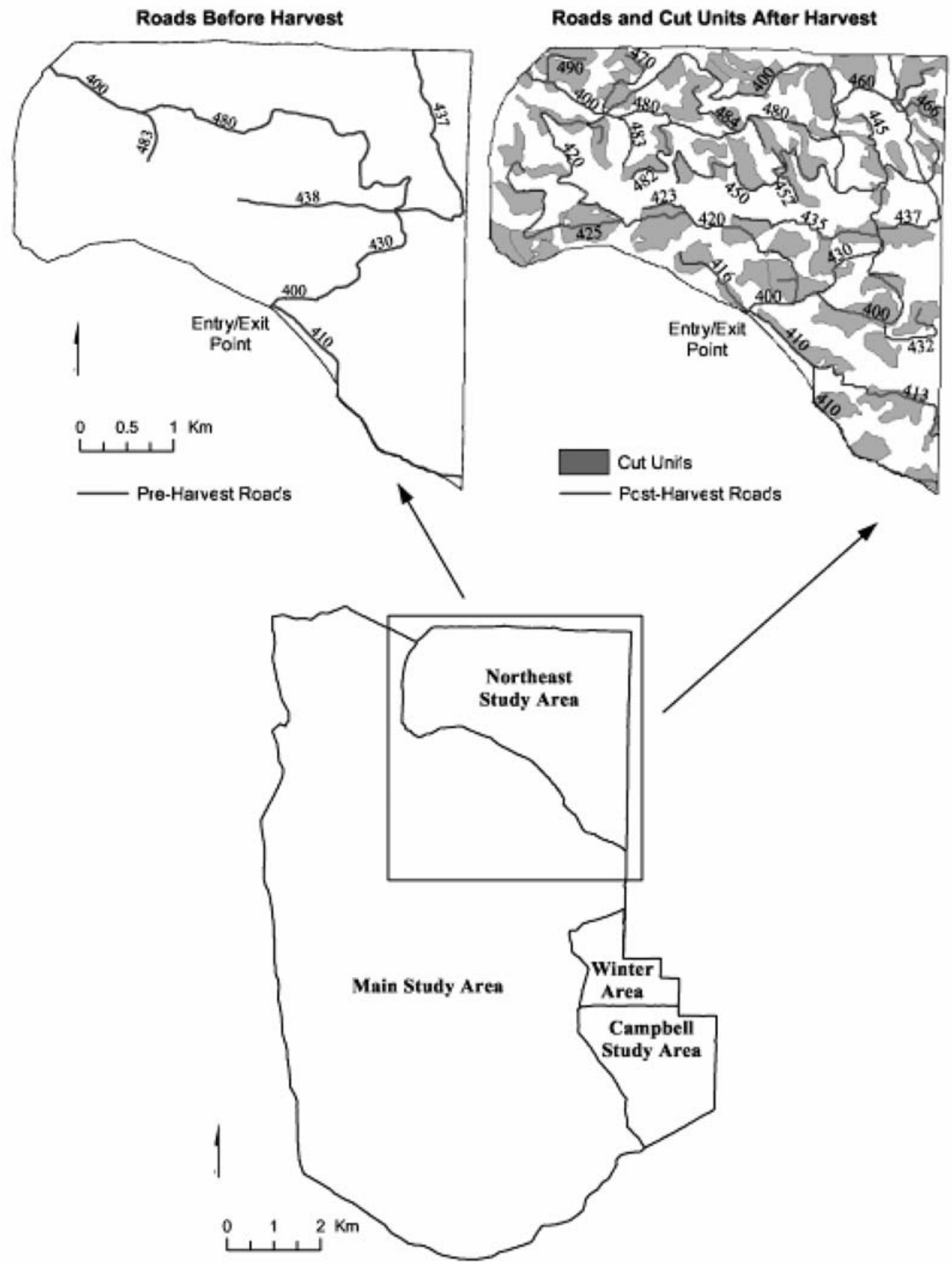

Figure 1. Northeast Study Area of Starkey, a 3,590-acre ungulate-proof enclosure, with roads before timber harvest (top left) versus roads and cut units after timber harvest (top right). The main haul routes used by log trucks during timber harvest (1992) included the 400, 420, 430, 437, 440, 460, and 480 roads that formed a set of interconnected loops spanning the inner portions of the study area (top right), and that led to the entry/exit point of the enclosure on its southwest boundary.

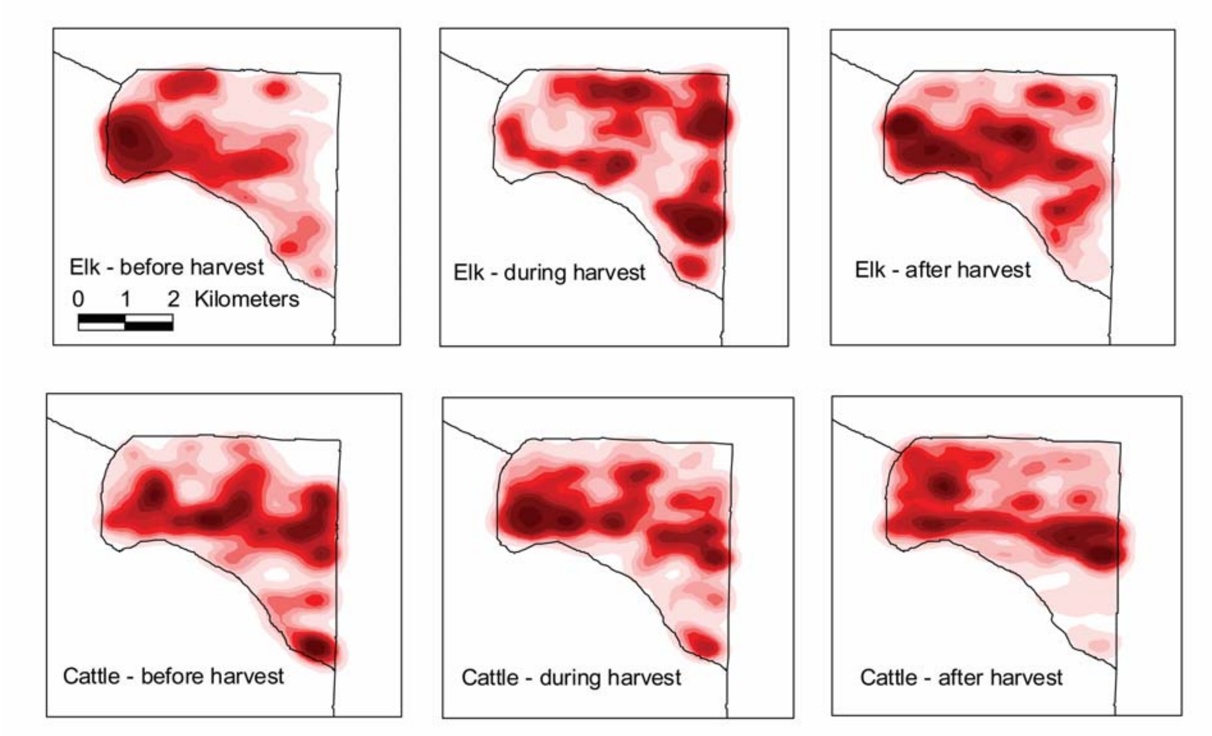

Figure 2. Spatial distributions of elk and cattle before (1989-1991), during (1992), and after (1993-1996) timber harvest, using fixed-kernel analysis of animal locations for each time period in the Northeast Study Area of Starkey Experimental Forest and Range, northeast Oregon.

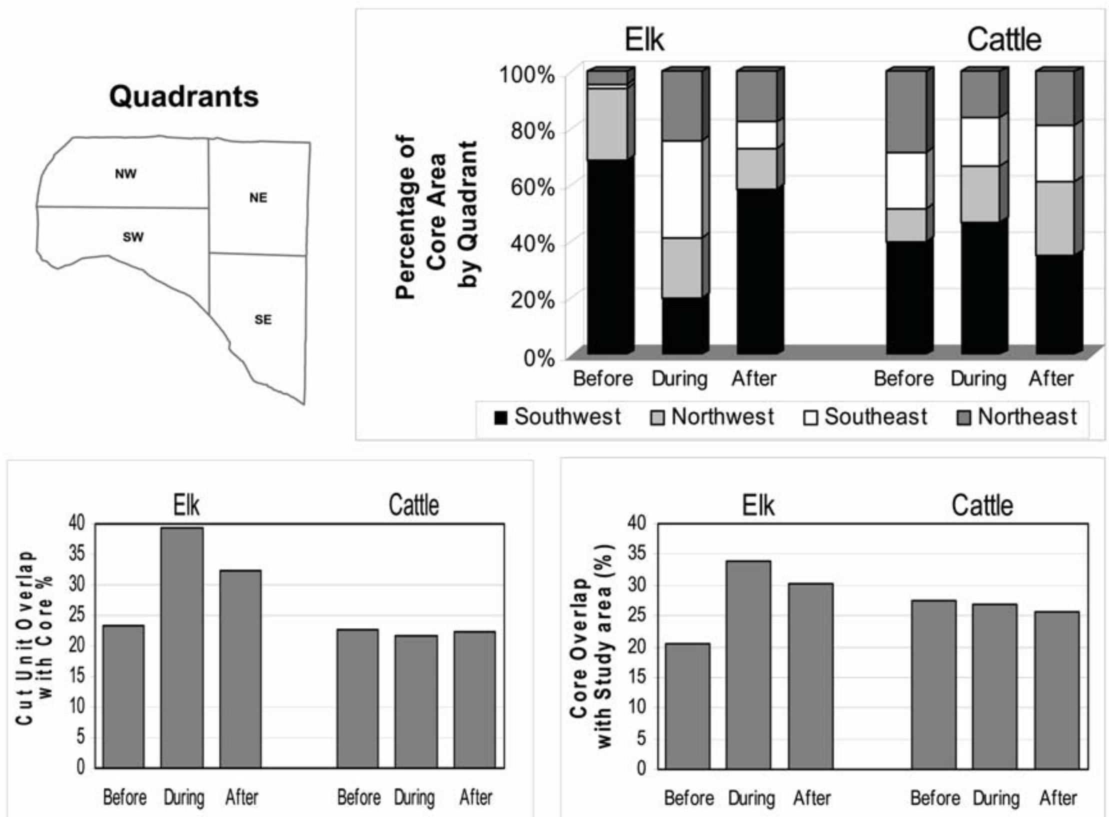

Figure 3. Percentage of the upper 50% of kernel volume, or 50% core area, of cattle and elk distributions occurring in each of four quadrants (top map) by time period (top right bar charts), the spatial overlap of timber harvest units, or cut units, within the 50% core area for each species (bottom left bar charts), and the percent area of the entire Northeast Study Area within the upper 50% of kernel volume, by time period and species (bottom right bar charts).

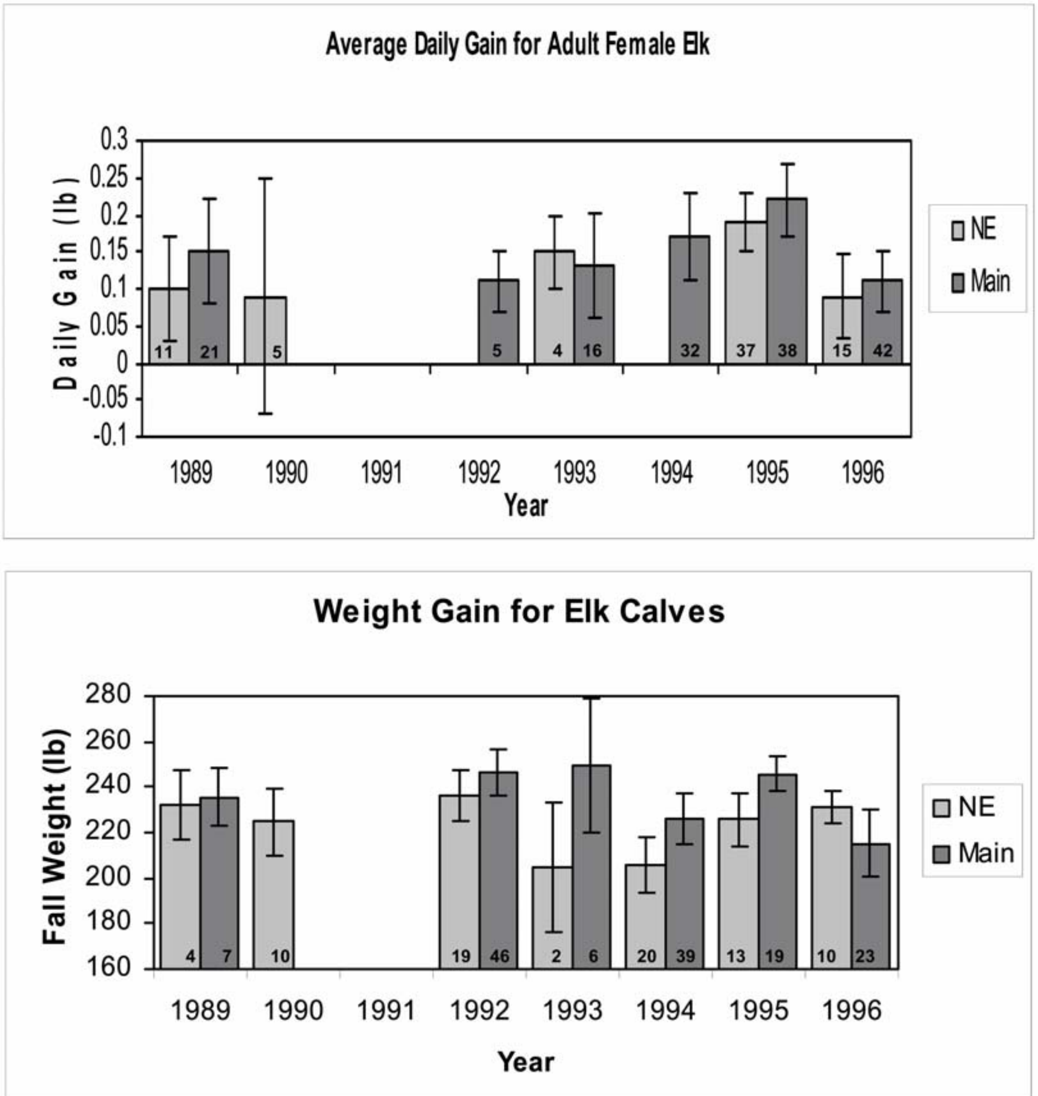

Figure 4. Mean weight gain by adult female elk and calf elk before (1989-1991), during, (1992), and after (1993-1996) timber harvest in the Northeast Study Area as compared to mean weight gain for the same years and age classes in the Main Study Area, Starkey Experimental Forest and Range, northeast Oregon. Error bars are the 95% percent confidence intervals about each mean. No weight data were available for cows or calves during 1991 in either study area, and for cows in Northeast Study Area during 1994. Data on the insufficient sample size of one cow elk weighed during 1992 in Northeast Study Area also was not included. Sample size (number of animals weighed) is shown at the bottom of each bar.

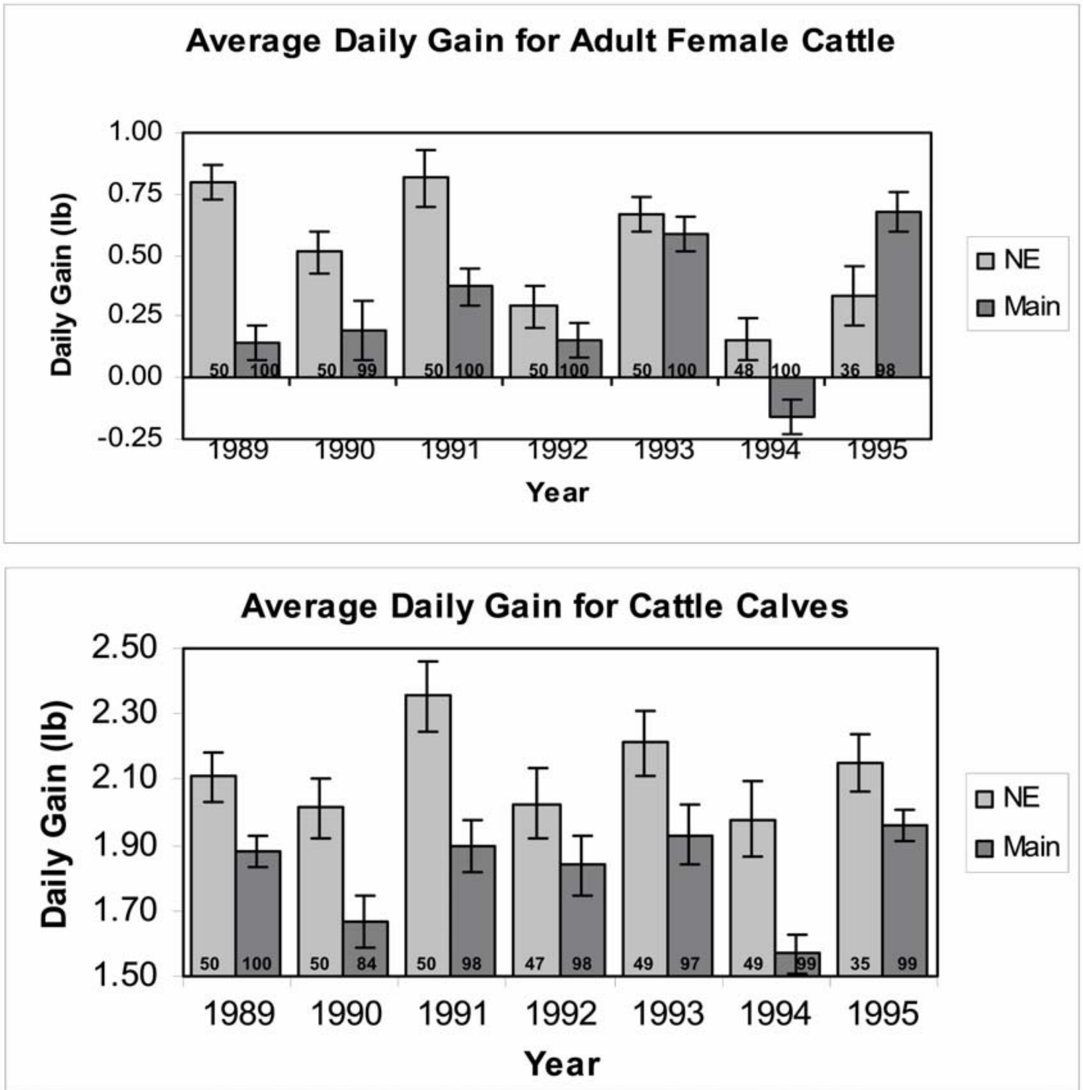

Figure 5. Mean weight gain by cattle, for adult cows and calves, before (1989-1991), during, (1992), and after (1993-1995) timber harvest in the Northeast Study Area as compared to mean weight gain for the same years and age classes in the Main Study Area, Starkey Experimental Forest and Range, northeast Oregon. Error bars are the 95% percent confidence intervals about each mean. Weight data for 1996 were not available. Sample size (number of animals weighed) is shown at the bottom of each bar.